



Glacial influence and stream macroinvertebrate biodiversity under climate change: Lessons from the Southern Alps

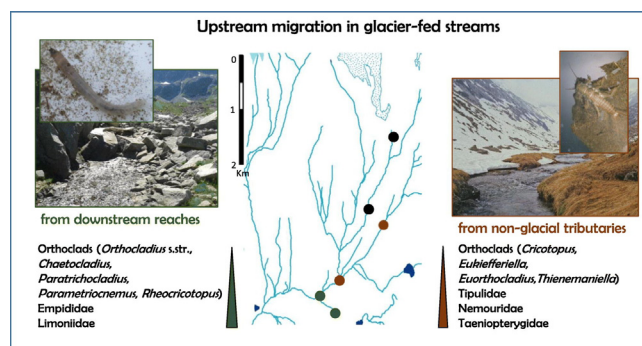
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HIGHLIGHTS

- The Alpine kryal is defined by mean Tmax ($<6^{\circ}\text{C}$) and % of *Diamesa* spp. ($>75\%$).
- *Diamesa* (*steinboeckii*, *goetghebueri*, *zernyi*) is the indicator taxon of glaciality.
- Glacial recession is causing glacier runoff and taxa richness and abundance changes.
- Obligate glacial river invertebrates disappear at glacier cover $<30\%$ and Tmax $>6^{\circ}\text{C}$.
- Orthoclads and nemourids migrate upstream to sites no longer exclusive to *Diamesa*.

GRAPHICAL ABSTRACT



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ABSTRACT

The aim of this work was to highlight the main ecological predictors driving invertebrate distribution in eight glacier-fed streams in the Southern Alps. Thirty-five sites belonging to four stream types were sampled monthly during the ablation season of one, two or three years between 1996 and 2014. Taxa from glacial (kryal and glacio-rhithral) and non-glacial (kreno-rhithral and lake outlet) sites were separated by canonical correspondence analysis (CCA) along a glacial influence gradient and a hydrological-altitudinal gradient. High glacial influence was associated mainly with low maximum water temperature (Tmax), high Glacial Index (calculated as a function of glacier area and distance from the glacier), and the abundance of *Diamesa* species (*D. steinboeckii*, *D. goetghebueri*, *D. zernyi*, and *D. latitarsis*). Change-point analysis and Threshold Indicator Taxa Analysis confirmed the CCA results in identifying these *Diamesa* species as the taxa with the strongest preference for high percent glacier cover in the catchment (change point $\sim 30\%$) and low Tmax (change point $\sim 6^{\circ}\text{C}$). Temporal changes in community structure were highlighted in seven sites fed by glaciers under different retreat rates. Where the rate was faster and the remaining glacier smaller ($<1\text{ km}^2$), the most cold-stenothermal kryal inhabitant, *D. steinboeckii*, almost disappeared or survived only as brachypterous populations, whereas other *Diamesinae* (*Pseudokiefferiella parva*), Orthocladinae (e.g. *Eukiefferiella*, *Orthocladus*), Limoniidae, Baetidae, Nemouridae, and non-insect taxa (e.g. Oligochaeta, Hydracarina) became more abundant. Upstream migration was observed in *Diamesa* spp. which conquered new stream reaches left free by the retreating glacier, and euricous taxa which colonized reaches with ameliorated environmental conditions, no longer the exclusive habitat of *Diamesa* spp. Co-occurrence of stochastic and deterministic assembly processes seem to drive spatio-temporal changes in these invertebrate communities. Long-term ecological studies on the adaptive biology of kryal species will be useful to predict the fate of Alpine biodiversity.

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1. Introduction

The atmospheric warming due to climate change experienced within the European Alps since the early 1980s is synchronous with warming globally, but its scale represents roughly a two-fold amplification of the global climate signal (Böhm et al., 2001; Casty et al., 2005). The warming, combined with decreased snowfall, has led to a 54% loss of ice area since 1850. Current projections suggest that just 4–13% of the 2003 European Alps ice area would remain by 2100 (Zemp et al., 2006; Huss, 2012). Glacier shrinking is more pronounced in the Southern Alps, where small glaciers (with a surface area < 1 km²) are expected to disappear within the next few decades (Beniston, 2006; Diolaiuti et al., 2012a). Therefore, small glaciers, due to their very rapid reaction time, are sites particularly suitable for assessment and monitoring of the impacts of climate change (Oerlemans and Fortuin, 1991; Diolaiuti et al., 2012b).

Understanding how climate change and, specifically, glacier retreat affect aquatic biodiversity in glacier-fed streams represents a future research challenge. Although research in this field has increased in the last five years (e.g. Jacobsen et al., 2012; Cauvy-Fraunié et al., 2015; Hotaling et al., 2017), to date, there is no literature referring to long-term ecological studies on the Southern Alps. Alpine streams with different water sources exhibit differences in hydrological regimes and the main physico-chemical features that support different plant and animal communities (Füreder et al., 2002). Glacially dominated rivers are characterized by the deterministic nature of benthic communities due to overriding conditions of low water temperature, low channel stability, low food availability, and strong daily discharge fluctuations associated with glacier run-off. A predictable longitudinal pattern of taxa richness and diversity, increasing with increasing distance from the glacier, has been described for many European glacier-fed streams (Castella et al., 2001), starting from the kryal sector (where maximum water temperature is below 4 °C), which is typically colonized almost exclusively by *Diamesa* species (Diptera: Chironomidae) (Lods-Crozet et al., 2001). Biodiversity increases with decreasing altitude and increasing distance from the glacier terminus, with a more diversified community in the glacio-rhithral, especially downstream of the confluence with tributaries fed by groundwater and rainfall (krenal and kreno-rhithral stream types) (Lencioni et al., 2007a). Non-glacial streams are typically characterized by transparent and cool waters (summer temperatures ranging from 2 to 15 °C), with low daily discharge fluctuations. They host a more diversified plant (algal mats and mosses) and animal community, co-dominated by the Chironomidae and EPT (Ephemeroptera, Plecoptera, and Trichoptera), than glacial streams (Milner et al., 2001).

Shrinking glaciers are resulting in the lengthening of glacier-fed streams (Finn et al., 2010; Robinson et al., 2014), with consequent: (i) upstream migration of specialist species to colonize the 'new' stream reach, still harsh, in front of the glacier terminus; and (ii) upstream migration of generalist species to sites with ameliorated environmental conditions due to reduced glacial run-off and increased temperature and channel stability (Hannah et al., 2007; Milner et al., 2009; Beniston and Stoffel, 2014; Cauvy-Fraunié et al., 2016). With the disappearance of glaciers, specialist cold stenothermal species may be seriously threatened with extinction concomitant with the disappearance of the kryal habitat (Khamis et al., 2014). However, the scale of these effects on stream biodiversity remains poorly quantified (Füreder, 2012), and how biotic interactions and community structure may be altered is not well understood (Khamis et al., 2015).

With the acceleration of glacier reduction, we may presume that associated biological processes could also be accelerated in glacier-fed streams in the Southern Alps. Therefore, the study of southern Alpine ecosystems provides opportunities for testing, within the scope of a few years, current predictive models.

The aim of this work was to highlight the main ecological predictors driving invertebrate distribution in eight glacier-fed streams with different sizes and rates of shrinkage. The selected streams and their non-glacial tributaries were particularly suitable for this aim, as they were

characterized by different glacial influence and length. The macroinvertebrate community structure of the glacial and non-glacial streams was analysed in relation to 13 environmental variables (glaciological, hydrological, and physico-chemical). The differential response and ecological thresholds of each species were evaluated along a gradient of glacial influence, as defined by the percentage of glacier cover and maximum water temperature.

Under global warming, species richness, population density, and diversity in biological traits of the kryal zoobenthic community are expected to increase as habitat conditions ameliorate (Brown et al., 2007; Jacobsen et al., 2014; Sertić Perić et al., 2015). Beta diversity may decrease as habitats become more homogenous, and gamma diversity may decrease as unique kryal stenoeicous species become extinct (Cauvy-Fraunié et al., 2015). This hypothesis was tested by examining macroinvertebrate colonization, after about two decades of glacial recession, in three glacier-fed streams studied for the first time at the end of the 1990s or in the early 2000s.

2. Material and methods

2.1. Study area

The study area was located in north-east Italy (46°N, 9–10°E; Trentino and Lombardy Provinces), within three protected areas: Adamello Brenta Nature Park (Adamello-Presanella mountains), Stelvio National Park (Ortles-Cevedale mountains), and Orobie Regional Park in the Orobian-Rhaetian Alps (Fig. 1). Thirty-five study sites were selected on 12 streams (Conca, Bedù, Conca tributary, Niscli, Cornisello, Vedretta outlet, Amola, Careser, Noce Bianco, Larcher, Trobio, and Gleno) located in four siliceous river catchments (Table 1).

Feeding glaciers have an area < 1 km², apart from Vedretta de la Mare (4.40 km²) and Careser (1.58 km²). They have all been subjected to generalised retreat with a glacier-retreat rate ranging from 0.2 (Conca) to 21.7 (Careser) ha/year from the end of the 1990s (Casarotto and Bertoni, 2015). Careser and Trobio have lost 67% and 80% of their area, respectively, in the last 15–20 years, with Trobio, covering a residual area of only 4.4 ha, almost disappearing (Smiraglia and Diolaiuti, 2015). The 35 study sites were selected from four habitat types reflecting stream origin according to Hieber et al. (2002) and Füreder et al. (2002): kryal (21 sites), glacio-rhithral (eight sites), kreno-rhithral (four sites), lake outlet (two sites) (Table 1). The uppermost reaches of the glacial streams (Conca, Niscli, Cornisello, Amola, Careser, Noce Bianco, and Trobio), fed only by melting ice and snow and located upstream of lakes and of the confluence with non-glacial tributaries, were classified as 'kryal'. The extension of the kryal varied from 50 m to 1.5 km according to the area of the feeding glacier, glacier run-off, thermal pattern, and input from main non-glacial tributaries. The downstream reaches of glacier-fed streams, classified as 'glacio-rhithral', were located generally downstream of a main non-glacial tributary and had a glacial origin, but were also fed by groundwater, snowmelt, and rainfall. The sites on non-glacial streams fed mainly by groundwater were classified as 'kreno-rhithral' (Conca tributary, Larcher, and Gleno), and those located on an outlet lake as 'lake outlet' (e.g. Vedretta Lake outlet). All 35 sites were above the treeline (1954–2833 m asl) and within 3 km downstream of the source, apart from C8 which was located on the Bedù stream, downstream of the confluence between Conca and Niscli streams, at 1300 m asl and 4.6 km from the Conca glacier terminus (Fig. 1).

All sites were sampled monthly (in June, August and September) during the ablation season of one, two or three years between 1996 and 2014. Sampling years and frequencies are shown in Table 1. Six sites were sampled twice, at intervals of nearly one or two decades after the first sampling (C0 and C2 on the Conca stream, after 17 years; V2 and V3 on the Cornisello stream, after 13 years; NB2 and NB3 on the Noce Bianco stream, after 9 years). One site, V0new, was sampled only in the most recent exercise. V0new was selected closer to the (retreating) Cornisello glacier (50 m) than the older uppermost site (V0, sampled

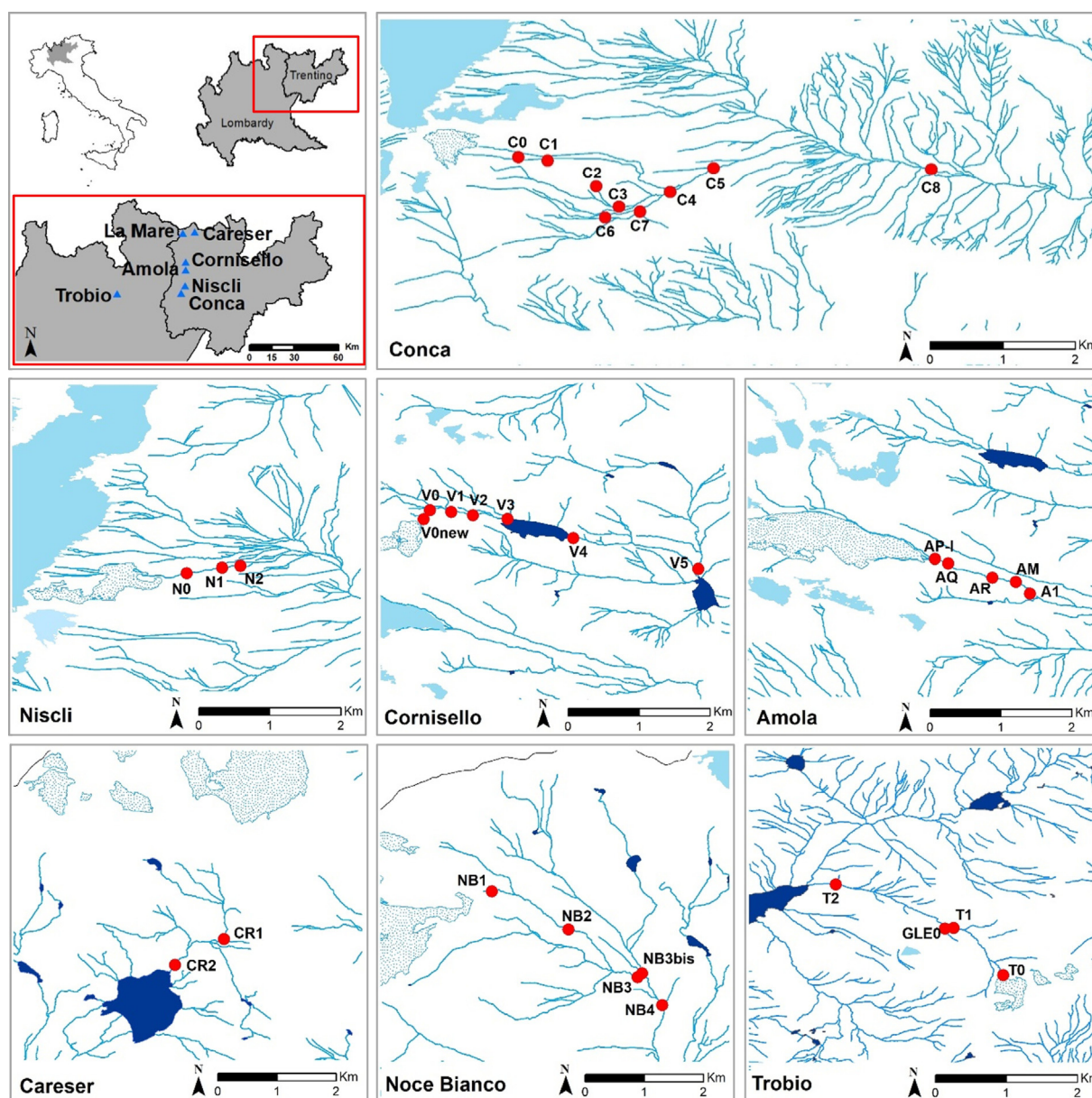


Fig. 1. The seven glacial systems studied in the Southern Alps.

only in 1997–1998, at 330 m from the glacier at that time). V0new was on the ‘new’ stream reach left free from ice cover by the retreated glacier. In 2010, V0 was omitted because it was found on a temporary stream channel.

2.2. Environmental data

Geomorphological (wetted channel width, sediment granulometry, and channel stability), hydrological (discharge, current velocity, and water depth), and physical and chemical data (water temperature, pH, conductivity, alkalinity, calcium, magnesium, sodium, potassium, reactive silica, sulphate, chloride, nitrate nitrogen, ammonium nitrogen, orthophosphate and total phosphorous, and suspended solids) were recorded in the benthic area according to Maiolini and Lencioni (2001).

Channel stability was assessed with the Pfankuch Stability Index (PSI; Pfankuch, 1975) that required scoring five variables (rock angularity, bed-surface brightness, particle packing, percentage of stable materials, scouring, and aquatic vegetation) with reference to the stream bottom component of the PSI. Scores were summed to provide an overall index

of channel stability, with a potential range of 15 to 60 (high scores representing unstable channels at the reach scale).

Discharge was measured as depth/velocity profiles with a current meter (OTT Hydrometrie Z30) at three transects per site or by the salt dilution method (Hongve, 1987). Along the same transects, granulometry was carried out by visual assessment of the percentage of five particle categories based on width (= *b*-axis): boulders (>20 cm), cobbles (5–20 cm), gravel (0.2–5 cm), sand (0.01–0.2 cm), and silt-mud (<0.01 cm).

Water temperature was monitored in each site at 1 h intervals from June to September with digital loggers (Gemini TinyTalkII, Gemini Data Loggers UK Ltd., Chichester, UK). Maximum water temperature (*T*_{max}) data were obtained from either continuous logging or during at least three 7-day periods in early summer, mid-summer, and early autumn.

Turbidity was measured as suspended solids, by filtering 250 (at glacial sites) and 2500 ml (at non-glacial sites) of water through 0.45-μm-membrane MFS filters and drying at 105 °C for 30 min. Conductivity, pH, and dissolved oxygen were recorded in the field using a field multi-probe (Hydrolab Quanta, Hydrolab Corporation®, Texas, USA). Nutrients, silica, and ions in 1 l of stream water were measured in the laboratory according to Standard Methods (APHA, 1992).

Table 1
Glacial systems investigated in the Southern Alps and Prealps (1996–2014): Conca (C), Niscl (N), Cornisello (V), Amola (A), Careser (CK), Noce Bianco (NB), and Trobio (T). Data for glacier area and altitude of the glacial snout are from the last year of sampling/catchment. Catchment area (km²) is calculated at the downstream site. Kyal sites: C0, C1, N0, N1, N2, V0, V0new, V1, V2, AP-I, AQ, AR, AM, A1, CK1, NB1, NB2, NB3, T0, T1; glacio-rhithral sites: C2, C3, C4, C5, C8, NB4, CK2, T2; kreno-rhithral sites: C6, C7, NB3bis, GLE0; lake outlet sites: V4, V5. Sampling years and frequencies*: J = June, A = August, S = September; if not specified, all sites in the different catchments were sampled in the specified year and season.

| | Conca | Niscl | Cornisello | Amola | Careser | Noce Bianco | Trobio |
|-----------------------------------|--|---------------------|---------------------------|---------------------|-----------------|---|-----------------------------|
| Mountain group | Adamello-Presanella | Adamello-Presanella | Adamello-Presanella | Adamello-Presanella | Ortles-Cevedale | Ortles-Cevedale | Ortles-Cevedale |
| River catchment | Sarca | Sarca | Sarca | Sarca | Noce | Noce | Serio |
| Catchment area (km ²) | 15.8 | 2.2 | 2.2 | 3.5 | 8.5 | 13.2 | 2.2 |
| Glaciers | 46°6'; 10°36' | 46°6'; 10°36' | 46°13'; 10°41' | 46°13'N; 10°40'E | 46°6'; 10°36' | 46°24'; 10°40' | 46°02'; 9°09' |
| Lat N; Long E | 0.14 | 0.43 | 0.49 | 0.82 | 4.83 | 4.4 | 0.04 |
| Glacier area (km ²) | 3031 | 2590 | 2900 | 2560 | 2860 | 2692 | 2550 |
| Altitude glacial snout (m asl) | 1300–2833 | 2372–2565 | 2139–2775 | 2421–2540 | 2642–2694 | 2270–2650 | 1954–2513 |
| Altitudinal range | | | | | | | |
| (m asl) | 350–4600 | 210–840 | 330–2980 | 50–1330 | 634–1841 | 60–2520 | 70–2300 |
| Distance from source (m) | 3; 9 | 1; 3 | 2; 7 | 1; 5 | 1; 2 | 2; 5 | 2; 4 |
| N. streams; N. sites | 2 kryal; 5 glacio-rhithral; | 3 kryal | 5 kryal; 2 lake outlet | 5 kryal | 2 kryal | 3 kryal; 1 glacio-rhithral; | 2 kryal; 1 glacio-rhithral; |
| N. sites/stream type | 2 kreno-rhithral | 1997 (JAS) | 1997 (JAS), 1998 (JAS), | 2014 (JAS) | 2001 (JAS) | 1 kreno-rhithral | 1 kreno-rhithral |
| Sampling years and frequencies* | 1996 (JAS), 1997 (JAS), 2013 (JAS; C0, C2) | | 2010 (JAS; V0new, V2, V3) | | | 2001 (AS), 2003 (JAS), 2010 (JAS; NB2, NB3) | 2013 (JAS) |

Standing crop of algae was estimated as chlorophyll *a* concentration by scraping, at each site and date, an area of 9 cm² from three stones selected randomly from the channel. Chlorophyll *a* was extracted with 90% acetone and the concentration was read at 665 and 750 nm according to Standard Methods (APHA, 1992).

During the second sampling exercise in the Conca, Cornisello, and Noce Bianco streams, only environmental data obtainable with the field multi-probe were recorded. For water temperature, continuous data were recorded with data loggers as in the first exercise.

Prior to benthic sampling in the 0.1 m² benthos replicates, current velocity was measured using a current meter (OTT Hydrometrie Z30) at 0.6 m depth at six random points around each area. The presence of mosses, lichens, and *Hydrurus foetidus* (Villars) Trevisan was evaluated by visual assessment according to Maiolini and Lencioni (2001). *H. foetidus* is a cold-adapted freshwater golden-brown alga common in glacier-fed streams.

Glacial influence was estimated with the Glacial Index (GI) and the percentage of glacier cover in the catchment (GCC). GI was calculated by combining glacier area with distance from the glacier terminus according to Jacobsen and Dangles (2012):

$$GI = \frac{\sqrt{\text{area}}}{\text{dist} + \sqrt{\text{area}}} \quad (\text{for area} > 0)$$

where 'area' is the extension of the glacier in km² and 'dist' is the distance in km of the study site from the glacier terminus. At maximum glacial influence (at zero distance from the glacier terminus), GI = 1, and it decreases exponentially towards zero with increasing distance from the glacier (Jacobsen and Dangles, 2012). GCC was estimated for each study site from GI according to Jacobsen et al. (2012):

$$GCC = 20.996e^{1.461GI}$$

GCC varies according to Glacial Index from 0 to 100%.

In Table 2, the main environmental features of the 12 study streams are reported.

2.3. Benthic macroinvertebrate collection and identification

The macroinvertebrate fauna was sampled between 1996 and 2014 in the 35 study sites on 12 streams (Table 1).

In each study site, benthic macroinvertebrates were collected by kick sampling 10 × 0.1-m² areas (replicates) within a reach 15 m in length according to Castella et al. (2001). The reaches were defined to represent the different sectors identified on the basis of valley and channel geomorphology. In each stream, the first reach was as close to the glacier terminus as possible. The second reach was typically within 1000 m of the glacier and upstream of any major tributary input. The downstream limit of the study sector was where a fully developed macroinvertebrate community occurred, i.e. where the Chironomidae were at least associated with EPT. This downstream limit was derived from preliminary surveys of the streams. Samples were taken from all microhabitat types (riffles, pools, etc.), in proportion to their frequency in the 15 m reach.

In exceptional circumstances, for example due to low water levels or snow cover, samples were replicated only five times within the 0.1 m² area, and were selected according to the same criteria. A 33 × 33 cm pond net with 250 μm mesh was used. Samples were filtered through a 250-μm mesh funnel to remove excess water and preserved in 75% ethanol.

Specimens were identified up to genus/species level (families Chironomidae and Simuliidae in the Diptera, Ephemeroptera, Plecoptera, and Trichoptera) or higher taxonomic levels (other Diptera, Coleoptera, Oligochaeta, Nematoda, Tricladida, Crustacea, and Hydracarina). All specimens (in 75% ethanol and on microscope slides) were deposited at the MUSE-Museo delle Scienze, Trento, Italy for archiving in the collection cINV0017. During sorting under the stereomicroscope (50×), coarse

Table 2

Environmental features (mean \pm SD) of the 12 study streams (only the variables with high correlations with the first two canonical correspondence analysis (CCA) axes are listed (scores > 0.5). GI = Glacial Index; altitude (Alt), distance from the source (Dist), channel stability (Pfank), maximum temperature (Tmax, °C), discharge (Disch, m³ s⁻¹), silica (SiO₂, mg l⁻¹), *Hydrurus foetidus* presence (Hydr).

| | GI | Alt | Dist | Pfank | Hydr | Tmax | Disch | SiO ₂ |
|-----------------|---------------|----------------|-----------------|-------------|---------------|----------------|-----------------|------------------|
| Cornisello | 0.7 \pm 0.2 | 2721 \pm 80 | 0.40 \pm 0.36 | 43 \pm 11 | 0.4 \pm 0.5 | 2.9 \pm 2.0 | 0.04 \pm 0.02 | 1.4 \pm 0.2 |
| Careser | 0.7 \pm 0.2 | 2668 \pm 37 | 1.24 \pm 0.85 | 52 \pm 2 | 0.0 | 5.7 \pm 1.9 | 1.25 \pm 0.13 | 1.9 \pm 0.1 |
| Noce Bianco | 0.7 \pm 0.2 | 2410 \pm 185 | 1.43 \pm 1.08 | 51 \pm 6 | 0.3 \pm 0.3 | 4.8 \pm 2.2 | 0.57 \pm 0.39 | 2.4 \pm 0.8 |
| Niscli | 0.6 \pm 0.2 | 2462 \pm 97 | 0.46 \pm 0.28 | 48 \pm 8 | 1.8 \pm 1.6 | 2.4 \pm 1.2 | 1.10 \pm 0.39 | 0.6 \pm 0.04 |
| Amola | 0.6 \pm 0.2 | 2481 \pm 48 | 0.71 \pm 0.52 | 40 \pm 4 | 1.7 \pm 0.4 | 1.7 \pm 1.4 | 0.26 \pm 0.13 | 1.1 \pm 0.1 |
| Conca | 0.3 \pm 0.2 | 2416 \pm 308 | 1.51 \pm 0.97 | 24 \pm 5 | 0.2 \pm 0.5 | 8.0 \pm 2.7 | 0.10 \pm 0.05 | 1.5 \pm 0.8 |
| Trobio | 0.3 \pm 0.2 | 2276 \pm 289 | 1.15 \pm 1.12 | 36 \pm 17 | 0 | 3.0 \pm 2.2 | 0.18 \pm 0.05 | 1.1 \pm 0.2 |
| Conca Bedù | 0.08 | 1300 | 4.60 | 25 \pm 2 | 0 | 11.1 \pm 3.2 | 1.09 \pm 0.25 | 2.3 \pm 0.5 |
| Vedretta outlet | 0 | 2360 \pm 339 | 0.75 \pm 0.97 | 26 \pm 6 | 0 | 8.3 \pm 0.5 | 0.02 \pm 0.02 | 2.2 \pm 0.9 |
| Conca tributary | 0 | 2228 \pm 81 | 0.45 \pm 0.37 | 25 | 0 | 5.6 \pm 1.0 | 0.02 \pm 0.01 | 2.9 \pm 0.2 |
| Larcher | 0 | 2270 | 2.52 | 28 | 0 | 9.8 \pm 2.1 | 0.30 \pm 0.05 | 5.0 \pm 0.2 |
| Gleno | 0 | 2343 | 0.50 | 18 | 0 | 0.6 \pm 0.3 | 0.03 \pm 0.02 | 2.7 \pm 0.5 |

benthic particulate organic matter (BPOM) was separated from each benthic replicate, dried at 60 °C and ashed at 500 °C in a muffle furnace.

2.4. Data analysis

The relationship between frequency and abundance of taxa was investigated. Rarity was defined as a taxon being found in <5% of the sampling units and making <5% of the total abundance for all sites combined (Robinson et al., 2016).

The diversity (alpha, beta, and gamma) of invertebrate communities was analysed at the level of catchment, stream type, sampling site, and year of sampling. Alpha diversity was estimated as number of species (S; local taxon richness), population density (N = ind m⁻²), and diversity by the Shannon-Wiener Index (H) (Shannon and Weaver, 1949). Taken dataset referred to glacier-fed streams (kryal and glacio-rhithral types). A linear regression analysis was performed to detect if glacial influence and distance from the glacier terminus were significant predictors of alpha diversity. Beta diversity was calculated as Whittaker's $\beta_w = \gamma / \bar{\alpha}$, where γ = gamma diversity (total number of species in the catchment) and $\bar{\alpha}$ = average number of species at the study sites (Whittaker, 1960). β_w was calculated by averaging data at stream level and for the stream types (kryal, glacio-rhithral, and non-glacial streams, with kreno-rhithral and lake outlet combined) to reduce variability due to stream length and number of study sites per stream. The software PAST 3.06 (Hammer et al., 2001) was used to calculate diversity and to perform the regression analysis.

Spatio-temporal differences in community structure between sites and dates were analysed using the Mann-Whitney non-parametric U test and the non-parametric ANOVA, the Kruskal-Wallis test (multiple comparisons of mean ranks for all groups). The relationships between environmental and biological variables were tested by means of Pearson's correlation. Values with $p < 0.05$ were considered significant. These analyses were performed using STATISTICA version 12.0 (@ Statsoft), also used to graphically represent spatial patterns in taxon richness.

To evaluate the distribution of taxa along environmental gradients, two types of analyses were performed: (i) canonical correspondence analysis (CCA) and (ii) change-point analysis (nCPA; Qian et al., 2003) combined with the Threshold Indicator Taxa Analysis (TITAN; Baker and King, 2010; Khamis et al., 2014).

CCA is a direct gradient analysis (or constrained ordination) that was carried out in this study to evaluate the impact of environmental variables (geographical, glaciological, hydrological, and physico-chemical variables) on the spatial and temporal distribution of macroinvertebrate species. Streams and the year of sampling were the factors used to interpret CCA results. Discarding highly correlated predictors ($r > 0.8$), 13 environmental variables were included in the first ordination analysis: altitude (Alt), distance from the source (Dist), glacial influence as Glacial Index (GI), glacier area (GI_area), channel stability (Pfank), maximum

water temperature (Tmax), discharge (Disch), turbidity as suspended solids (SS), pH, conductivity (Cond), silica (SiO₂), chlorophyll *a* (Chl) and the presence of *H. foetidus* (Hydr). Hydr was included as the dummy variable defined by the following codes: 0 = absent, 1 = scarce (present in about 30% of replicates), 2 = present in about 50% of replicates, 3 = very abundant (present in >75% of replicates).

TITAN and nCPA are two non-parametric statistical approaches used to detect changes in taxa distribution along an environmental gradient over space, highlighting transition points (i.e. zones of rapid change) in a biological community in response to small, continuous increases in an environmental 'stressor'. In the present study, they have been applied as tools for identification of ecological thresholds along a gradient of glacial influence (i.e. the stressor) as defined by GCC and Tmax. Community thresholds are represented as: (i) TITAN thresholds, synchronous changes in the abundance of $z -$ or $z +$ taxa within a narrow range of the glacial influence or thermal gradient; (ii) candidate change points in nCPA identified via deviance reduction of Bray-Curtis distance values.

Specifically, TITAN orders and partitions observations along the gradient using Indicator Value (IndVal) scores (Dufrêne and Legendre, 1997) to define groupings. The IndVal of a species is the degree to which a species is an indicator of the conditions found in a group of sites. The indicator value of species 'i' for group 'j' is obtained with the equation:

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$$

where ' A_{ij} ' is the proportion of the individuals of species 'i' that are in group 'j' and ' B_{ij} ' is the proportion of sites in group 'j' that contain species 'i'.

Multiple candidate change points were identified and indicator value scores calculated for each taxon (250 permutations). Declining ($z -$) and increasing ($z +$) taxa were used to identify community-level change points and uncertainty was estimated via bootstrapping (500 replicates). For nCPA, candidate change points were assessed via deviance reduction with the assumption that the mean and variance of the Bray-Curtis distance would respond to compositional changes. The 'change point' separates observations into two groups and deviance reduction is used to identify the most homogenous two groups. The final change point represents the most homogenous two groups based on 500 bootstrapped replicates. The best split is the one for which deviance reduction (i.e. the difference between the deviance of the whole population and the sum of the deviances of the two separate groups) is the highest (Qian et al., 2003).

For CCA, TITAN, and nCPA analyses, quantitative faunal data, expressed as total invertebrate density (ind m⁻²) per sampling unit (site \times month \times year), were $[\log(x + 1)]$ transformed prior to analysis for normalization. Rare taxa were excluded from the biological matrix. The list of taxon codes, species names, and authors are in Table S3.

These analyses were performed using R (version 3.2.4 Revised for Windows, R Development Core Team, 2014, <http://www.R-project.org>); for CCA, the *cca* function in the *vegan* package was used (Dixon, 2003).

3. Results

3.1. Macroinvertebrate community: structure and diversity in the stream types

The 1050 samples from the 35 sampling sites included 181,515 invertebrates belonging to 114 taxa. The dipteran family Chironomidae, with 66 taxa (58% of the identified taxa) and 137,818 individuals (76% of collected animals), was the dominant group.

Forty-two (35%) taxa were found in <5% of the sampling units, and 20 (17%) were exclusive to one sampling unit (*Eusimulium* sp., *Potamophylax cingulatus*, Hydraenidae family, and 17 Chironomidae species). Taxa more frequent (found in >40% of sampling units) and abundant (with >5% of the total abundance for all sites combined), in descending order of total abundance, were: *Diamesa zernyi* gr., *D. steinboeckii*, *D. goetghebueri*, *Baetis alpinus*, and *D. cinerella* gr. (Fig. S1). Thirty-seven taxa were rare.

Shannon-Wiener Index increased significantly with increasing distance from the glacier terminus, in spite of the specific longitudinal pattern in local diversity differing between the eight streams (linear regression model: slope $a = 0.423$, intercept $b = 1.130$, $r = 0.66$, $p = 0.0001$; Fig. 2 A).

Local taxon richness was also correlated significantly with distance from the glacier terminus ($r = 0.61$; $p < 0.0001$), GI ($r = -0.78$; $p < 0.0001$), Tmax ($r = 0.60$; $p < 0.0001$), Pfanck Index ($r = -0.48$; $p < 0.0001$), and glacier area ($r = -0.26$; $p = 0.0042$). Specifically, GI explained 61% of the variability in local taxon richness, following an exponential fit (Fig. 2 B). Gamma diversity also decreased with increasing GI in sites dominated by glacier run-off (Table 3). All sampling units collected from sites classified as 'kryal' according to origin, were grouped on the right part of the diagram (GI = 0.35–0.97; S/sampling unit = 2–23). Only T1 was grouped on the left side (GI = 0.16; Fig. 2 B), because it was fed by the smallest glacier (glacier area = 0.04 km²). Kryal sites were located mainly within 1.5 km from the glacier terminus, with Tmax from 0.6 °C to 9.1 °C and channel stability from 'excellent' (Pfanck Index = 18) to 'poor' (Pfanck Index = 60).

All sampling units collected in the sites classified as 'glacio-rhithral' were grouped on the left side of the diagram (GI = 0.08–0.28; S/sampling unit = 9–54), apart from CR2 and NB4, both with GI = 0.5, because they were fed by the largest glaciers (glacier area ≥ 4.4 km²). Glacio-rhithral sites were located mainly at a distance of >1 km from the glacier terminus, with Tmax up to 15.4 °C. Most of these sites were in Conca, the stream where the highest alpha and gamma diversity and the lowest turnover were recorded (Table S1). Glacio-rhithral sites were richer in taxa than non-glacial sites (Table 3), because of the harsh habitat conditions of some kreno-rhithral sites fed by groundwater (e.g. GLE0, at 2343 m asl, with Tmax = 1 °C and Smax = 5 taxa).

Because of the high environmental heterogeneity of the kryal sites associated with a wide range of GI and Tmax values (Fig. 2 B), and high beta diversity of this stream type ($B_w = 4.23$), three kryal classes were defined based on GI: class 1 with $GI \geq 0.8$; class 2 with $0.6 \leq GI < 0.8$; and class 3 with $GI < 0.6$. The total and mean number of taxa increased from class 1 to class 3 (Table 3), but the macroinvertebrate community of the three classes, independent of GI, was dominated by the genus *Diamesa* (Diamesinae; Chironomidae), accounting for a mean of $\geq 75\%$ of the fauna (Fig. 3). The significant differences between the other two stream types were in the percentages of Chironomidae (<60%), Diamesinae (<25%), and *Diamesa* (<25%). Glacio-rhithral and kreno-rhithral sites differed in the percentage of *Diamesa*, which was higher in the former (25%) than in the latter (10%) (Fig. 3). Fig. 4 shows the percentages of Chironomidae, Diamesinae, and *Diamesa* spp. increasing with

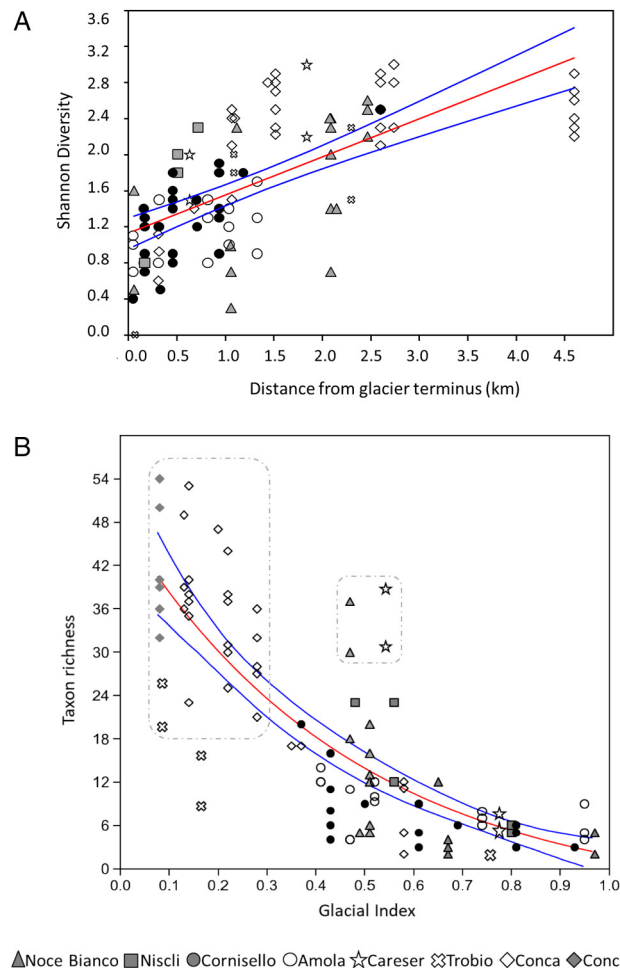


Fig. 2. A. Longitudinal change in invertebrate community diversity in the eight glacier-fed streams plotted according to distance downstream of glacier terminus (blue line = 95% confidence intervals; $R^2 = 0.61$). B. Local macroinvertebrate taxon richness in the eight glacier-fed streams as a function of Glacial Index (GI) (29 study sites, 99 sampling units, rare species included). The regression line is an exponential model (blue line = 95% confidence intervals; $R^2 = 0.61$). In the two frames, sampling units of sites classified as 'glacio-rhithral' according to the origin. Different shapes represent different streams.

increasing GI, reaching 99–100% of *Diamesa* spp. in kryal sampling units with $GI > 0.4$. The percentage of *Diamesa* spp. ($R^2 = 0.512$) described this trend better than the percentages of Diamesinae ($R^2 = 0.438$) and Chironomidae ($R^2 = 0.207$).

3.2. Macroinvertebrate community structure in relation to environmental variables: spatial patterns and ecological thresholds

The CCA conducted to explore the simultaneous effects of the 13 environmental variables on macroinvertebrate communities gave four eigenvalues (CCA1 = 0.429, CCA2 = 0.141, CCA3 = 0.062, CCA4 = 0.058), explaining overall 69.2% of the total faunal variance.

The variables associated most with changes in macroinvertebrate communities (in order of decreasing importance based on their scores) were: GI, presence of *Hydrurus*, altitude, suspended sediments, and channel stability, negatively correlated with CCA axis 1; distance from the source, Tmax, and silica, positively correlated with CCA axis 1; and discharge, positively correlated with CCA axis 2. For altitude and distance from the source, a high correlation (score ≥ 0.6) was seen also with CCA axis 2 (Table S2, Fig. 5). The first axis defined a glacial influence gradient, while the second axis defined a hydrological-altitudinal gradient.

Table 3

Alpha, beta, and gamma diversity of the main stream types defined on the basis of their origin. Because of the high variability between the 23 kryal sites, three classes were distinguished on the basis of Glacial Index (GI) values. Dist = distance from the source (km).

| Stream type | N | Dist (km) | GI | Gamma | Beta | Taxon richness (alpha) | | |
|------------------------------|---|-----------|----------------|-------|-------------|---------------------------|--------|-----|
| | | | | | | Mean \pm SD | Min | Max |
| KRYAL (GI \geq 0.8) | 7 | 0.05–1.08 | 0.8 ± 0.1 | 22 | 3.0 | 7 ± 4 | 2 | 14 |
| KRYAL ($0.6 \leq$ GI < 0.8) | 5 | 0.38–2.10 | 0.5 ± 0.05 | 35 | 2.3 | 15 ± 7 | 9 | 25 |
| KRYAL (GI < 0.6) | 9 | 0.71–1.33 | 0.3 ± 0.1 | 64 | 2.9 | 22 ± 7 | 11 | 34 |
| GL-RHY | 8 | 1.13–4.60 | 0.2 ± 0.1 | 104 | 1.9 | 56 ± 13 | 32 | 71 |
| NON-GL ^a | 6 | 0.06–2.52 | – | 79 | 2.25 (1.92) | 35 ± 21 (41 \pm 17) | 5 (23) | 63 |

^a Values calculated omitting GLEO.

CCA axes 1 and 2 separated the sites into roughly three groups: the kryal sites on the left (II–III quadrant), most of which were located on the streams Cornisello, Careser, Noce Bianco, Amola, Niscli, and Trobio; the glacio-rhithral sites on the upper right (I–IV quadrant), most of which were located on the Bedù and Conca streams; the kreno-rhithral and lake outlet sites (III–IV quadrant), located on the Conca tributary, Larcher, Gleno, and Vedretta Lake outlet (Fig. 5). The taxa best associated with kryal sites were cold stenothermal species of the genus *Diamesa*: *D. steinboeckii*, *D. goetghebueri*, *D. latitarsis* gr. (mainly represented by *D. latitarsis* sensu stricto), *D. zernyi* gr. (mainly represented by *D. zernyi*), *D. cinerella* gr. (mainly represented by *D. tonsa*), and *D. bertrami* (Fig. 5, Table S3). The taxa best associated with glacio-rhithral sites included the chironomid subfamilies Orthoclaadiinae (e.g. *Parametrioctenemus stylatus*, *Rheocricotopus effusus*) and Tanypodinae (e.g. *Zavrelimyia* sp.), and other Diptera (e.g. *Simulium* spp. and Tipulidae) and EPT (e.g. Nemouridae, Chloroperlidae, Perlodidae, Heptageniidae, and Rhyacophilidae). Many rheophilous species, such as *Epeorus alpicola*, *S. argyreatum*, and *Boreoheptagya monticola*, in this area were highly positively correlated with CCA axis 2 (Fig. 5, Table S3). The taxa best associated with kreno-rhithral and outlet sites were the Simuliidae (*Prosimulium* spp.), Diamesinae (e.g. *Pseudodiamesa branickii*), Orthoclaadiinae (e.g. *Chaetocladius*, *Corynoneura*, *Eukiefferiella*, *Orthoclaadius*, *Paratrachoclaadius*, and *Thienemanniella*), and Chironominae (*Micropsectra atrofasciata* gr.). Some species were highly associated with two stream types. For example, *Pseudokiefferiella parva* and *Prosimulium latimucro* were common in non-glacial and kryal sites, while *B. alpinus*, *Protonemoura* spp., and *Perlodes intricatus* were common in glacio-rhithral and kreno-rhithral sites.

Using TITAN analysis, changes in community composition were identified at thresholds of <31.1% glacier cover and <5.6 °C maximum temperature. The nCPA analysis highlighted peaks at similar points along the glacial influence gradient (29.6%) and thermal gradient (5.3 °C) suggesting a threshold change in the community composition (Fig. S2).

Results from the TITAN analysis broadly confirmed the CCA results, selecting *Diamesa* species as the taxa with the strongest preference for

high GCC and low Tmax. Specifically, the abundance of *D. steinboeckii*, *D. zernyi* gr., *D. goetghebueri*, and *D. latitarsis* gr. increased significantly with increasing GCC ($z +$ taxa, above ~30% GCC; Fig. 6 A). The same set of $z -$ taxa without *D. latitarsis* gr. was observed for the thermal gradient (Fig. 6 B): *D. steinboeckii*, *D. zernyi* gr., and *D. goetghebueri* decreased significantly above Tmax about 6 °C. Other *Diamesa* species, such as *D. cinerella* gr. and *D. bertrami*, were favoured by high GCC and low water temperature but were not significantly selected as threshold taxa for these conditions. This is probably because of the high frequency of these two taxa also in non-glacial sites. The other taxa for which significant change points were identified decreased in abundance across the glacial influence gradient ($z -$ taxa) (Fig. 6 A) and increased in abundance across the thermal gradient ($z +$ taxa) (Fig. 6 B). For glacial influence, two main change points were evident for z -taxa, at 0% (taxa exclusive of non-glacial habitats) and at ~10%, with a synchronous decline > 20%. For water temperature, two main change points were evident for z -taxa, at ~2 °C (taxa frequent in kryal habitats among which was *D. latitarsis*), and a synchronous increase over ~6 °C.

3.3. Temporal changes in the macroinvertebrate community structure

Within one to two decades, the three feeding glaciers lost from 6 to 7% (Cornisello and Noce Bianco) to 22% (Conca) of their area, with consequent lengthening of the streams by 60 m (Noce Bianco), 245 m (Cornisello), and 370 m (Conca) (Table 4). Run-off decreased by 27% in Conca, while it has remained almost constant in Cornisello and has nearly doubled in Noce Bianco. Maximum water temperature increased in the Conca sites (by 0.4–0.5 °C) and slightly decreased or has remained constant in the other two streams. GI decreased only in the Conca sites, halving in site C0. The progressive reduction of glacial influence in the Conca sites was also highlighted by the CCA analysis, with increasing correlation of C2 with CCA axis 1 and C0 with CCA axis 2 (Table S4).

In all streams, invertebrate population density (ind m⁻²) increased with sampling year ($r > 0.4$, $p < 0.03$) and was almost four times higher in C2, 17 years after the first sampling exercise. This increase was due to the increase of non-insect taxa (Hydracarina in all streams; Tricladida, Nematoda, Oligochaeta, and Harpacticoida in Conca), the Chironomidae and Limoniidae (in all streams), and *Prosimulium rufipes* and EPT (e.g. *Protonemura* spp. and *B. alpinus*; in Conca).

Gamma diversity increased by 2 units in Noce Bianco, 5 units in Cornisello, and 9 units in Conca (Table 4). Macroinvertebrate community composition changed in line with altered environmental conditions, with changes in the relative abundance of different taxa and the discovery of new taxa and the disappearance of others. At least a five-fold increase or decrease in taxon abundance relative to the first sampling exercise was considered a change. As a consequence of different retreat rates of the feeding glaciers, these changes, whose evaluation included rare taxa, affected local richness (S) and beta diversity in the three systems in different ways (Table 4).

The main changes in community composition were observed in the two Conca sites (Figs. 4 and 7). At both sites, the Chironomidae continued to be the dominant taxon (>50%) in the community after 17 years, but within the family, the balance between subfamilies changed in favour of the Orthoclaadiinae, becoming more prevalent at 1.4 km from

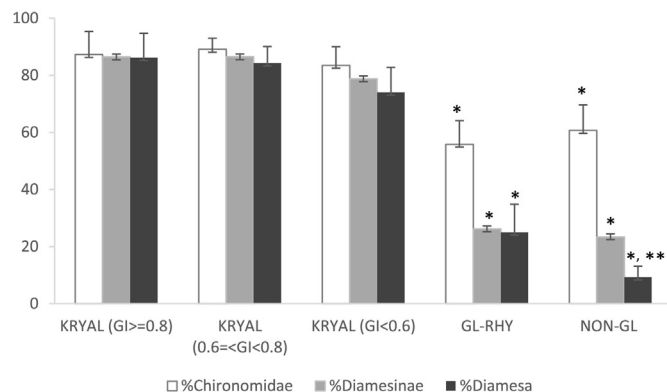


Fig. 3. Mean \pm SE percentage of Chironomidae, Diamesinae and *Diamesa* spp. in the different stream types (defined according to the source). * = significant difference respect to kryal sites, ** significant difference respect to glacio-rhithral sites. GL-RHY = glacio-rhithral. NON-GL = kreno-rhithral and lake outlet.

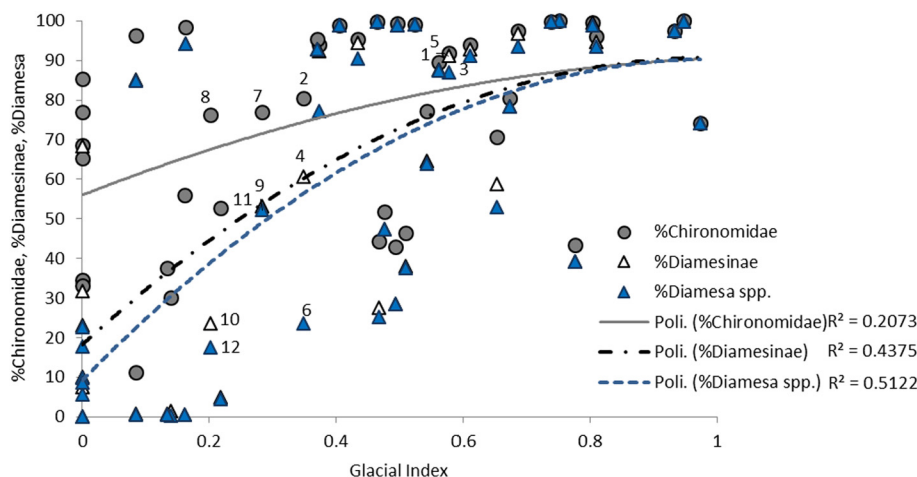


Fig. 4. Local percentage of Chironomidae, Diamesinae and *Diamesa* spp. in the 12 streams as a function of Glacial Index (GI) (35 study sites, 120 sampling units, rare species included). The regression line is an exponential model. Non-glacial units (GI = 0) are on the y-axis. Numbers refer to the two sites (C0, C2) for which the most obvious changes were highlighted. % Chironomidae: 1 = C0_1996–97, 2 = C0_2013; 7 = C2_1996–97, 8 = C2_2013; % Diamesinae: 3 = C0_1996–97, 4 = C0_2013; 9 = C2_1996–97, 10 = C2_2013; % *Diamesa*: 5 = C0_1996–97, 6 = C0_2013; 11 = C2_1996–97, 12 = C2_2013.

the glacier terminus (C2, Fig. 4). At the species level, the main changes were: the strong contraction of the *D. steinboeckii* population, which fell to 11% of the Diamesinae in C0 and disappeared in C2; the strong increase in *P. parva* at both sites, and in *D. latitarsis* gr., *D. zernyi* gr., and *D. cinerella* gr. in C2; and the increase in *Euorthocladus rivicola* gr. in C0 and in several species of *Eukiefferiella*, *Tvetenia*, *Orthocladus* s.str., *Corynoneura*, *Heleniella*, *Krenosmittia*, *Parorthocladus*, and

Thienemanniella in C2 (Table S5). Some of these trends were common to the other sites, such as the general increase in *D. cinerella* gr. (apart from in V0new), *D. zernyi* gr., and *D. latitarsis* gr. (apart from in the Noce Bianco). The community found in V0new was dominated by *D. steinboeckii* (90%), resembling that was found 13 years ago in V0 where *D. steinboeckii* represented 89% of the community.

At catchment level, even when the sites sampled only in the first exercise are included, eight new species were found in Conca and three in Cornisello. The new findings were all in the subfamilies Orthocladiinae and Diamesinae. Other species, listed in Fig. 8, were found as new in only one site, but they were present downstream or in the non-glacial tributary in the first sampling exercise. Upstream migration to uppermost kryal sites was highlighted for 22 insect taxa, mainly the Chironomidae, followed by other Diptera (e.g. Limoniidae), and Plecoptera (Nemouridae and Taeniopterygidae) (Fig. 8). Some species were found at an altitude of 400–500 m higher than in the first exercise, such as *P. stylatus*, *E. rivicola* gr., and *Nemoura mortoni*. The distance covered by these species was 1.0–1.4 km.

Some taxa were found only in the first exercise, at catchment or site level (Table S5). Among these, *P. latimucro* seemed to disappear in all streams. NB3 was the site where the highest percentage (35%) of species, mainly Plecoptera (*Protonemura* sp. and *Leuctra* sp.), were lost concurrently with increased glacier run-off.

4. Discussion

This study found a highly diverse and spatially-structured macroinvertebrate assemblage in Alpine high-altitude streams, with the dipteran family Chironomidae predominating, as expected (Lencioni et al., 2007a). Glacial Index, ranging from 0 in non-glacial habitats to ~1 in kryal habitats, was one of the most robust predictors of taxon richness and spatial distribution of macroinvertebrates. Only when the feeding glacier was very small (with an area $\ll 1$ km²), did the distance from the glacier terminus alone become the best predictor of glaciality. Specifically, high GI, along with low water temperature, low silica content, high channel instability, high turbidity, and high abundance of *H. foetidus*, characterized the headwaters of the studied glacier-fed streams (kryal), making these habitats 'extreme' for life (Lencioni, 2004). In the Southern Alps, 'low' and 'high' values for Glacial Index and water temperature correspond to different values from those reported as typical for the kryal (Milner and Petts, 1994). In fact, the Alpine kryal may exhibit a GI of 0.16 and Tmax of 9 °C, values more typical of the glacio-rhithral, and, in the case of temperature, also of non-glacial sites (Jacobsen et al., 2012). The main reasons are the small area of the feeding glaciers (e.g.

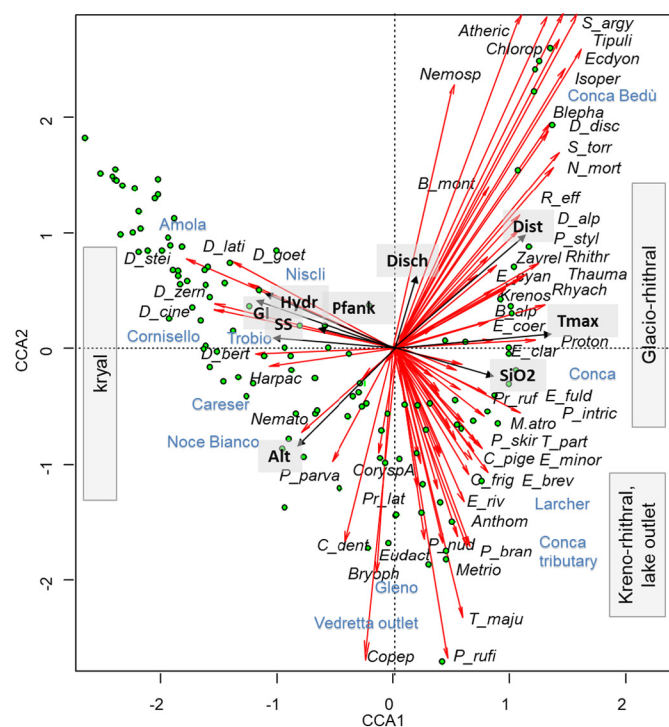


Fig. 5. Canonical constrained ordination diagram. Environmental variables are shown as black arrows, species as red arrows and sampling units as green circles. GI = Glacial Index; Alt = altitude, Dist = distance from the glacier terminus, Pfrank = channel stability, Tmax = maximum water temperature, Disch = discharge, SS = turbidity as suspended sediments, SiO₂ = silica, Hydr = *Hydrurus foetidus* presence, *Epeorus alpicola* is not represented because of its high scores with CCA axis 1 (=1.6) and CCA axis 2 (=3.4). Only environmental variables with scores ≥ 0.5 and taxa with scores ≥ 0.6 , with at least one of the two first CCA axes are reported. Species codes are in Table S3. Faunal variance explained: CCA axis 1 = 42.9%, CCA axis 2 = 14.1%; total inertia = 2.226.

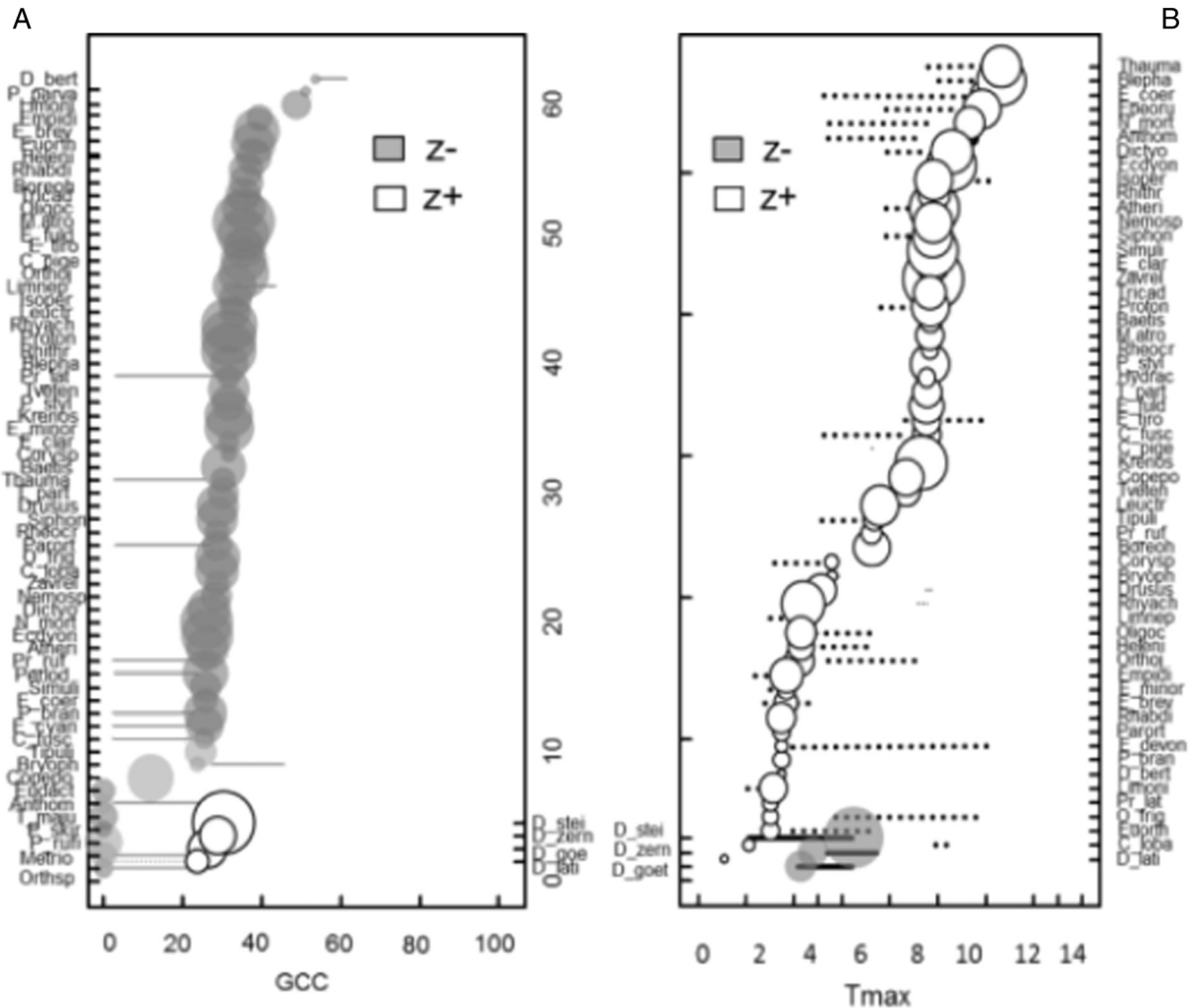


Fig. 6. Significant indicator taxa (TITAN, $P < 0.05$, purity $N = 0.95$) identifying glacier influence gradients (glacier cover in catchment; GCC) (A) and maximum water temperature (T_{max}) (B) for the seven glacial systems. Grey symbols represent negative indicator taxa (i.e. abundance declined) and white indicate positive taxa (i.e. abundance increased). Change point symbols are sized in proportion to response (z scores). Horizontal lines represent 5th and 95th percentiles from 500 bootstrap replicates. See Table S3 for full taxonomic names.

Conca and Trobio), low discharge (e.g. Conca and Cornisello), and stream flow on dark roche moutonnées (e.g. Conca). Specifically, a stream flowing over a roche moutonnée branches out into small rivulets that warm up on the bedrock. These reaches also have atypically high channel stability (Pfankuch Index < 30). Mean T_{max} throughout was $< 6^{\circ}\text{C}$, and

this may be considered the upper thermal limit of the kryal in the Southern Alps.

The observed pattern of longitudinal distribution of species resembled the model described by Castella et al. (2001), starting from the kryal sector colonized almost exclusively by *Diamesa* species, known to

Table 4

Alpha (α = total taxon number), N = total abundance (ind m^{-2}) and β = beta for the six sites resampled after 9–17 years and the new site V0new. Environmental variables: GI = glacial index; T_{max} = maximum water temperature ($^{\circ}\text{C}$); GI_{area} = glacier area (km^2); $Snout_alt$ = altitude of the snout (m asl); Length = Lengthening (m) of the stream; Runoff = discharge (l s^{-1}) at the uppermost site of the stream. Data referred to α , N , β , Runoff and T_{max} refer to the same weeks of sampling in different years.

| Site | Year | GI | T_{max} | GI_{area} | $Snout_alt$ | Length | Runoff | α | N | β | γ^a |
|-------|---------|-----|-----------|-------------|--------------|--------|--------|----------|------|---------|------------|
| C0 | 1996–97 | 0.6 | 3.0 | 0.18 | 2994 | | 41 | 16 | 975 | 0.5 | 91 |
| C2 | 1996–97 | 0.3 | 9.4 | | | | | 47 | 2043 | | |
| C0 | 2013 | 0.3 | 3.5 | 0.14 | 3031 | 370 | 30 | 17 | 1746 | 0.6 | 100 |
| C2 | 2013 | 0.2 | 9.8 | | | | | 47 | 7617 | | |
| V0 | 1997–98 | 0.7 | 2.3 | | | | 48 | 6 | 248 | 0.3 | 28 |
| V2 | 1997–98 | 0.6 | 3.7 | 0.52 | 2876 | | | 17 | 255 | | |
| V3 | 1997–98 | 0.4 | 7.5 | | | | | 22 | 1144 | | |
| V0new | 2010 | 0.9 | 1.2 | | | 245 | 47 | 3 | 410 | 0.4 | 33 |
| V2 | 2010 | 0.5 | 3.5 | 0.49 | 2900 | | | 9 | 1360 | | |
| V3 | 2010 | 0.4 | 6.0 | | | | | 20 | 2610 | | |
| NB2 | 2001 | 0.7 | 6.5 | 4.75 | 2670 | | 448 | 7 | 50 | 0.7 | 56 |
| NB3 | 2001–03 | 0.5 | 7.6 | | | | | 34 | 107 | | |
| NB2 | 2010 | 0.7 | 6.6 | 4.40 | 2692 | 60 | 800 | 12 | 170 | 0.5 | 58 |
| NB3 | 2010 | 0.5 | 7.0 | | | | | 5 | 70 | | |

^a Gamma (γ) diversity refers to the catchment.

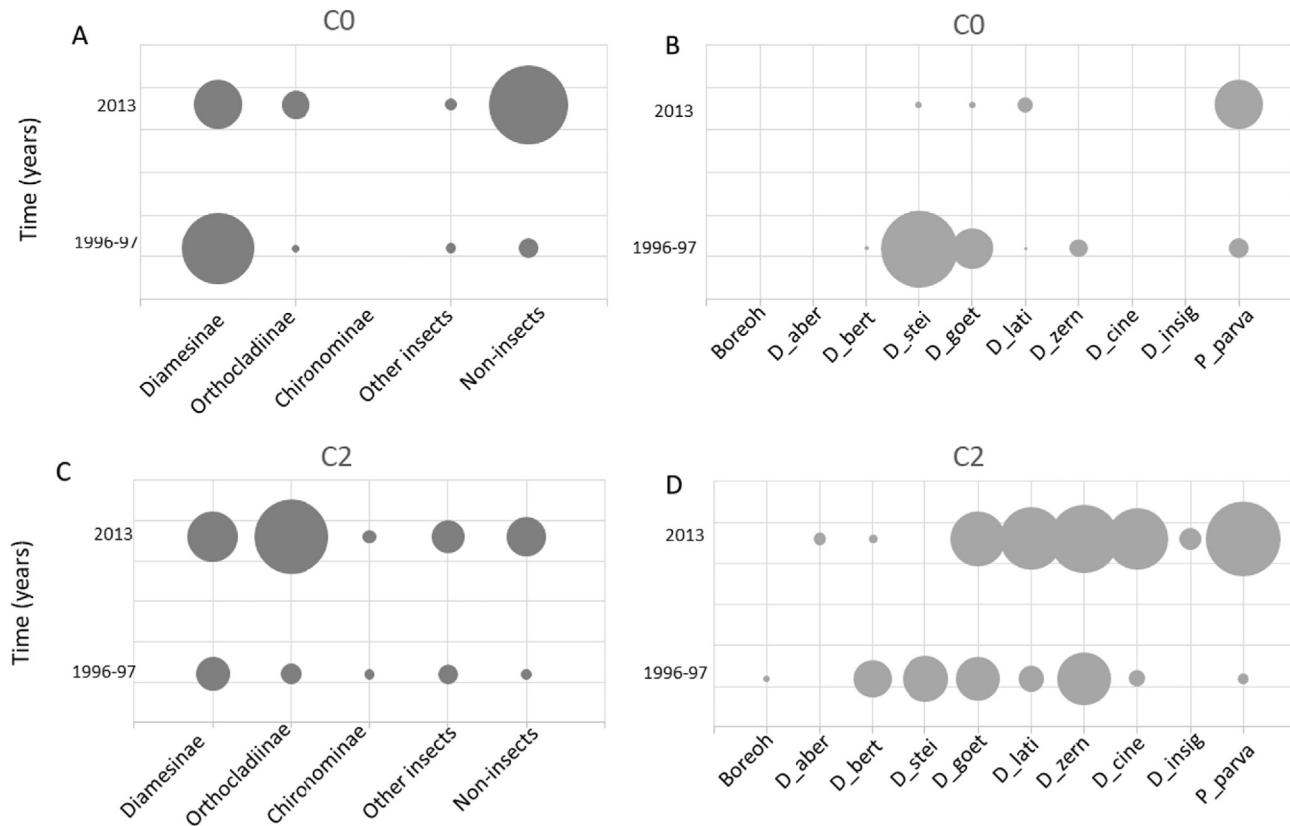
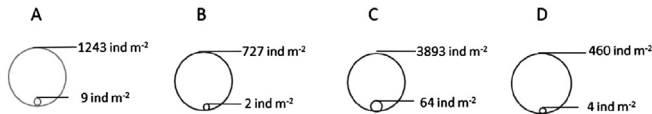


Fig. 7. Relative abundances of Chironomidae subfamilies, insects other than chironomids, and non-insect taxa (left), relative composition of Diamesinae (right) in C0 (A, B) and C2 (C, D) sampled after about two decades (1996–1997 and 2013). *Diamesa dampfi* was omitted in graph D, because it was found in C2 only in the first sampling exercise with <1 ind m⁻². Species codes are in Table S3. Dot size refers to benthic fauna density and is in proportion to the abundance (ind m⁻²) of the single taxon, comparable within a site.



be adapted to a variety of environmental rigors such as freezing and scarcity of food (Lencioni et al., 2015). Biodiversity increased with decreasing altitude and increasing distance from the glacier terminus, with a more diversified community in the glacio-rhithral, especially downstream of the confluence with non-glacial tributaries, as expected (Lencioni et al., 2007b). In milder conditions (at higher temperature, lower turbidity, etc.), at a distance from the glacier terminus of >1 km, the Orthocladinae likely outcompeted *Diamesa* spp. and became the dominant Chironomidae subfamily in the stream. The Tanypodinae, Chironominae, other Diptera, and EPT became progressively more abundant with increasing distance from the glacier and decreasing GI, as also observed by other authors in European glacier-fed streams (e.g. Füreder et al., 2002).

The present study found the relative abundance of *Diamesa* spp. to be the best biological parameter for separating the streams with different origins in the Southern Alps: ≥75% in the kryal, ~25% in the glacio-rhithral, and ~10% in the non-glacial streams. Unlike in previous studies (Lods-Crozet et al., 2001; Lencioni et al., 2007b), *D. zernyi* gr. co-dominated the Alpine kryal habitat with the most typical 'glacial' *Diamesa* species (i.e. *D. steinboeckii*, *D. goetghebuerei*, and *D. latitarsis*). The *zernyi* group is generally associated more with spring-fed streams, along with *D. cinerella* and *D. bertrami* (Lencioni et al., 2007a). *D. steinboeckii*, *D. zernyi* gr., *D. goetghebuerei*, and *D. latitarsis* gr. were selected by the multivariate and TITAN analyses as best indicators of glaciality. Specifically, TITAN analysis emphasised clear community change points for the thresholds defined by GCC = ~30% and Tmax = ~6 °C. Previous studies suggested a slightly higher value of GCC (approximately 50%) below which obligate glacial river macroinvertebrates begin to disappear and generalist taxa

become more prevalent (Jacobsen et al., 2012). These data also confirmed the strong cold stenothermy of *D. steinboeckii*, *D. zernyi* gr., and *D. goetghebuerei* (Lencioni et al., 2007a), was apparently stronger than that of *D. latitarsis* gr. (represented mainly by *D. latitarsis* and *D. modesta*), which was unexpectedly, was not found in the group of taxa associated with temperatures lower than 6 °C. These results may explain the increasing abundance of *D. latitarsis* gr. in kryal sites found warmer after one to two decades.

There was a tendency towards rarity, with few species frequent and abundant in all sampling units (i.e. *D. zernyi* gr., *D. steinboeckii*, *D. goetghebuerei*, *D. cinerella* gr., and *B. alpinus*). A high degree of rarity and few species in common between headwaters have also been observed by other authors (Lencioni et al., 2011; Cauvy-Fraunié et al., 2015; Robinson et al., 2016). This may be because of the insularity of stream networks and catchments in alpine landscapes and the harsh environmental conditions associated with glacial origin. The same reasons may explain the high environmental heterogeneity observed in kryal sites with high values of beta diversity, as previously reported for some Pyrenean streams (Finn et al., 2013). Different degrees of dispersal limitation within catchments were demonstrated by beta diversity in the 12 streams, with stronger limitation in catchments with higher inter-site heterogeneity (e.g. in Trobio and Noce Bianco).

Dispersal occurs via insect adults flying overland and by aquatic instars of all macroinvertebrates moving through the hyporheic zone (Lencioni and Spitale, 2015), or by drift and upstream movement in the stream (Brittain and Eikeland, 1988; Lencioni et al., 2006). Dispersal is influenced by many stochastic factors such as wind (for adult flight)

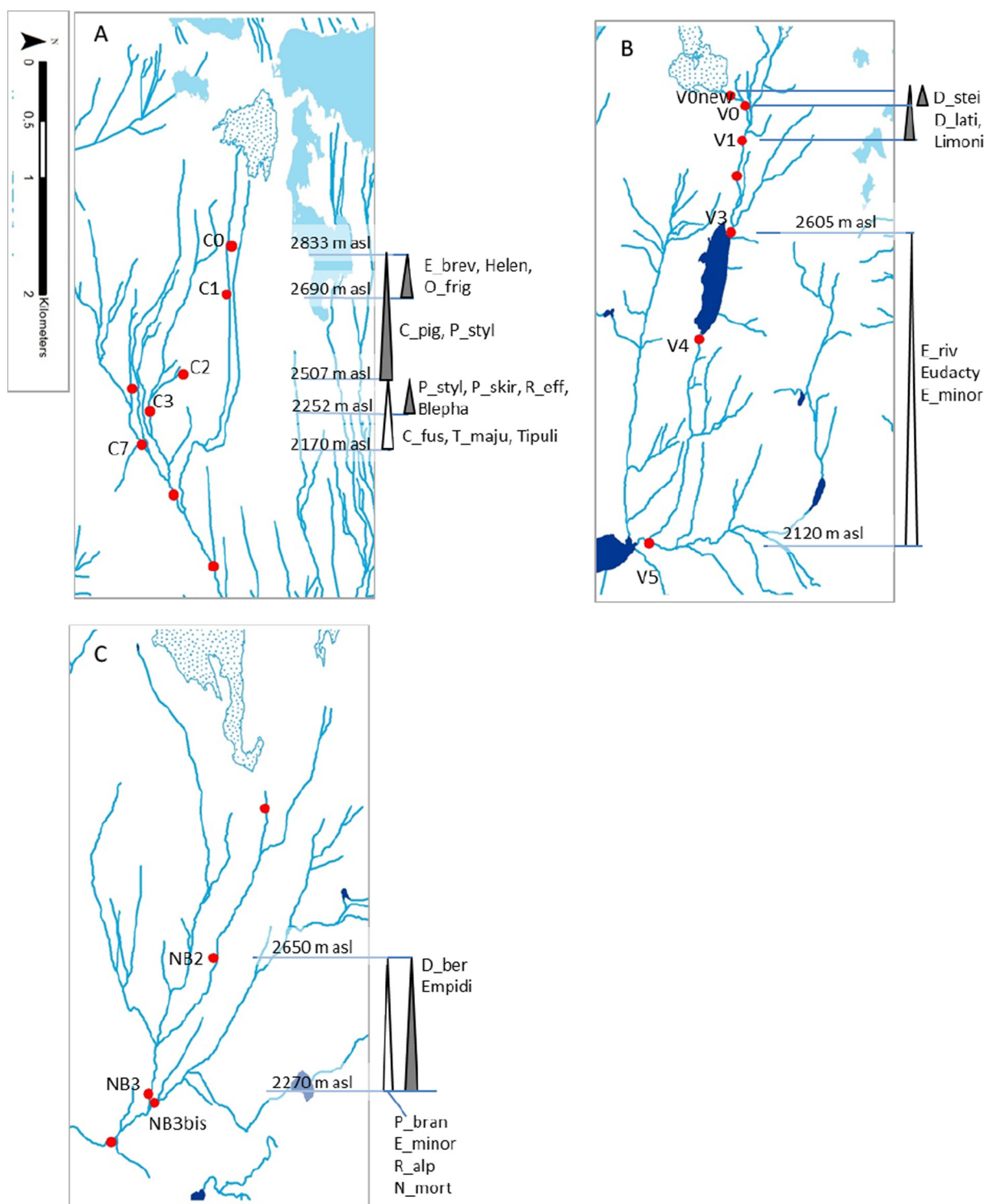


Fig. 8. Taxa migration in Conca (A), Cornisello (B) and Noce Bianco (C) streams. Grey cones = upstream migration from glacial sites; white cones = migration from non-glacial sites. Species codes: Blepha = Blephariceridae, C_fus = *Cricotopus fuscus*, C_pig = *Chaetocladius piger* gr., D_ber = *Diamesa bertrami*, D_lati = *Diamesa latitarsis* gr., D_stein = *Diamesa steinboeckii*, E_brev = *Eukiefferiella brevicar*, E_minor = *Eukiefferiella minor* gr., Empidi = Empididae, E_riv = *Euorthocladius rivicola* gr., Eudacty = *Eudactylocladius* spp., Helen = *Heleniella* spp., Limoni = Limoniidae, N_mort = *Nemoura mortoni*, O_frig = *Orthocladius frigidus*, P_bran = *Pseudodiamesa branickii*, P_skir = *Paratrachocladius skirwithensis*, P_styl = *Parametrioctenemus stylatus*, R_alp = *Rhabdiopteryx alpina*, R_eff = *Rheocricotopus effusus*, Tipuli = Tipulidae, T_maju = *Thienemanniella majuscula*.

and winter duration and snowpack cover (for all aquatic instars) (Petersen et al., 2004), with strong inter-annual variation (Lencioni, 2004). In fact, different meteorological conditions in successive years may affect phenology, altering life cycles (Lods-Crozet et al., 2012). Therefore, it is possible to find different developmental stages of the same species or even different species in the same month in different

years. It is possible that some species may have been overlooked during one of the two sampling exercises in the present study, making it difficult to explain the 'disappearance' and 'appearance' of species in the three streams. All the 'lost' and 'new' species were rare. Among these, some were semi-aquatic species (e.g. *Parasmittia* sp., *Pseudosmittia holsata*, and *Gymnetriocnemus* sp.), with only 1–2 individuals collected from

each during sampling. Being taxa associated with the margins of water habitats, their presence in the samples could be considered accidental. Conversely, the increase or decrease in abundance of some taxa may be explained on the basis of changes to their autecological features in response to altered environmental conditions under glacier retreat (e.g. increased run-off or increased water temperature). An example is the strong population contraction of the ‘ice fly’ *D. steinboeckii* in the Conca stream, fed by the glacier that underwent the strongest retreat in the last 17 years. *D. steinboeckii* is considered the ‘flagship’ species of the Alpine kryal (Lencioni et al., 2007a), and its disappearance at 1.4 km from the glacier terminus in the Conca stream should be interpreted as a warning signal. In the uppermost sites of glacier-fed streams fed by ‘ghost’ glaciers and with an area $\ll 1 \text{ km}^2$, such as the Trobio (4.4 ha), isolated brachypterous populations of *D. steinboeckii* still persist. These glaciers are expected to disappear in a few decades, and this species, with an exceptionally low dispersal capacity because of the wingless adults, is at serious risk of extinction. Additionally, the limited availability of kryal habitats, especially breeding habitats, fed by small glaciers increases the probability of hybridization between different congeneric species. This was observed in the Trobio stream, where a morphological hybrid between *D. tonsa* and *D. vaillanti* was found. Among *Diamesa* species, *D. cinerella* gr. and *D. zernyi* gr. seem better able to withstand glacier recession; for these species, a significant decrease has not been recorded yet in any of the three streams in which sampling was repeated after one to two decades.

For many taxa, upstream migration was observed from downstream glacio-rhithral sites or from the main non-glacial tributaries where these taxa were collected in the first sampling exercise. Among these were many dipterans, especially in the Chironomidae (e.g. *P. parva* and many Orthocladiinae), as well as the Empididae, Limoniidae, Tipulidae, and other insects such as the plecopteran family Nemouridae. Therefore, functional diversity increased in kryal sites, as expected (Ilg and Castella, 2006; Brown and Milner, 2012), because new colonizers possessed traits (e.g. feeding habits, metamorphosis type) different from those in taxa already present. For example, kryal sites found in the first sampling exercise to be occupied almost exclusively by holometabolous grazers (scrapers) Diamesinae have been invaded by shredders (e.g. *N. mortoni*), predators (e.g. Empididae, Hydracarina), and detritus feeders (e.g. Oligochaeta). Apart from the Diptera, all the other new colonizers have incomplete metamorphosis or no pupation. Functional redundancy also increased because of the arrival of many other grazers (mainly Orthocladiinae). This redundancy may contribute to the resilience of ecological communities to further ecosystem changes.

The most obvious environmental and biological changes were observed in the Conca stream fed by the glacier undergoing the most rapid retreat among those studied. According to Cauvy-Fraunié et al. (2015), this system seems to be in the last phases of retreat (i.e. with increasing water temperature and decreasing run-off) and the Noce Bianco in the initial phase (i.e. with decreasing water temperature and increasing run-off). However, the trend in diversity expected in relation to the shrinking phase (Finn et al., 2013; Jacobsen et al., 2014; Cauvy-Fraunié et al., 2015) was not observed. Specifically, gamma diversity is not yet decreasing in Conca, because kryal species are still surviving close to the glacier terminus together with typical rhithral taxa. The arrival of these more eurieicous species close to the glacier terminus suggest ameliorated environmental conditions, probably also because of a high amount of debris from the banks (Cauvy-Fraunié et al., 2016). Among these were, *D. aberrata* and *D. insignipes*, previously collected only in springs rich in mosses (Lencioni et al., 2011).

Identification to species level, difficult to achieve especially for the Chironomidae in the larval instar stages, is crucial for understanding spatio-temporal changes in Alpine macroinvertebrate communities. Adult identification is recommended; otherwise there is a risk that some kryal species may disappear before being known to science. This is highlighted by the discovery, only in 2014 after almost 20 years of sampling in the area, of *D. martae* Kownacki & Kownacka, 1980, a species

new to Italy, and *D. nowickiana* Kownacki & Kownacka, 1975, a species new to the Trentino Province, by identifying two adult specimens crawling on the Amola glacier.

5. Conclusions

As habitat conditions change in space and time, macroinvertebrate community structure in glacier-fed streams changes in relation to the co-occurrence of stochastic and deterministic assembly processes. Due to their sensitivity and high resilience, remote aquatic ecosystems in the Southern Alps are suitable for assessment and monitoring of the effects of climate change on macroinvertebrate communities.

Biota living in kryal habitats is extremely specialized and has developed unique survival strategies to withstand environmental constraints that could be modified due to climate change. One research priority is simply understanding the relationships between the speed of climate change and glacier shrinking, and the speed with which kryal species need to adapt to environmental changes (Li et al., 2016). In this respect, *Diamesa* species, expected to be lost as glaciers disappear and water temperature increases, are excellent indicators of environmental changes.

Conclusions about changes in biodiversity in changing habitats must be cautious. Long-term ecological research and studies on the adaptive biology of kryal species (e.g. dispersal propensity, thermo-tolerance, genetic diversity, and the capacity to exploit refugia), are useful for predicting the fate of Alpine biodiversity, endangered also by other stressors. Among these stressors are pesticides accumulating in ice meltwaters and personal care products transported by wind (Chiogna et al., 2016). A future challenge will be to study the effects on glacial biodiversity of these and other chemical contaminants in combination with increasing temperature.

Conflict of interest

The author declares that there are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2017.11.266>.

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